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A new genus and species of damsel-dragonfly from the Middle Jurassic of Inner Mongolia (Odonata: Campteroptlebiidae)

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The Campteroptlebiidae is the largest family of fossil damsel-dragonflies, containing more than 60 species described from Lower Jurassic–Lower Cretaceous strata of Europe and Asia. This group is especially diverse in the Middle–Late Jurassic strata in Inner Mongolia, northeastern China, with some very large species (Zhang *et al.*, 2006, 2008, 2013; Nel *et al.*, 2007, 2008, 2009; Petrulevičius *et al.*, 2011; Li *et al.*, 2013; Zhang *et al.*, 2013; Zheng *et al.*, 2016, 2017). Thus it is surprising that we found a new representative of these damsel-dragonflies, belonging to a group of genera characterized by a very particular shape of the forewing cubito-anal area. This fossil has a unique shape of the forewing median vein, allowing its attribution to a new genus and species. It increases our knowledge about the palaeobiodiversity of this impressive group of Odonata.

Material and methods

The specimen is a damsel-dragonfly forewing collected from the Middle–Upper Jurassic Haifanggou Formation at Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China. The photograph of the whole specimen was taken using a Canon 5D camera. The specimen was examined dry and under alcohol, using a stereo microscope. The photographs were prepared using a digital camera connected to a Zeiss Discovery V16 microscope. The specimen is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

We follow the higher classification of fossil and extant Odonoptera based on the phylogenetic system of Bechly (1996, 2008), with the dragonfly wing venation nomenclature used in this paper based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993), Bechly (1996), and Jacquelin *et al.* (2018). We deny any

value to the interpretation of Trueman & Rowe (2019a) that Nel *et al.* (2019) already discussed. The answer of Trueman & Rowe (2019b: fig. 1) is erroneous, especially in their interpretation of the anal and cubital veins for which these authors used a campteroptlebiid forewing in which these two veins are distally fused and not a hindwing in which these two veins are not fused as it was clearly indicated by Nel *et al.* (2019). As a consequence, the very strong convex vein CuA of Isophlebioidea has simply no name or need to be considered as a secondary vein under Truman & Rowe's (2019a, b) interpretation, which is clearly erroneous. The error of these last authors stems probably from a poor knowledge of the fossil record of the Odonoptera. We note that in our re-interpretation of the venation of the Palaeozoic *Enigmaptera magnifica* of Trueman & Rowe (2019b: fig. 4), some important veins remain without any name, while all are clearly explained in Nel *et al.* (2019).

Venation abbreviations are as follows: AA anterior anal; Arc arculus; Ax primary antenodal crossvein; C costa; CuA anterior cubitus; IR intercalary radial vein; MAa anterior branch of anterior media; MAb posterior branch of anterior media; MP posterior media; Pt pterostigma; RA anterior radius; RP posterior radius; Sn subnodal crossvein; ScP posterior subcostal.

Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Isophlebioptera Bechly, 1996

Superfamily Isophlebioidea Handlirsch, 1906

Family Campteroptlebiidae Handlirsch, 1920

Genus *Azarphlebia* gen. nov.

Type species. *Azarphlebia evanescens* sp. nov.

Etymology. Named after our friend and colleague Prof.

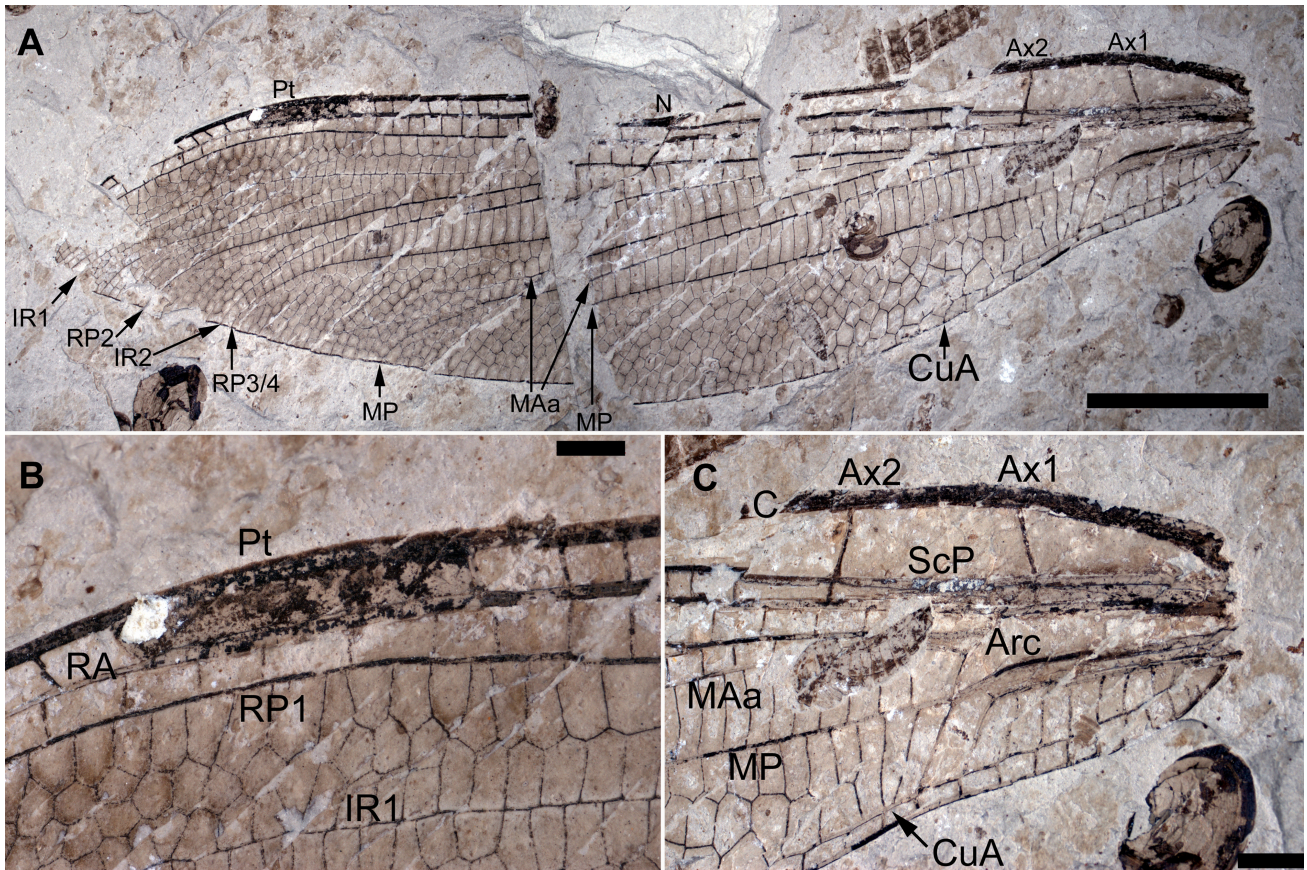


FIGURE 1. *Azarphlebia evanescens* gen. et sp. nov., holotype NIGP173379. **A**, Forewing. **B**, Pterostigma. **C**, Forewing base. Scale bars: 10 mm (**A**), 2 mm (**B** and **C**).

Dany Azar and the suffix ‘*Phlebia*’, frequently used for the Campteropteroptera. Gender feminine.

Diagnosis. Forewing characters only. MAa distally zigzagged and vanishing in area between MP and RP3/4 (autapomorphy); pterostigma elongate but rather broad, covering five cells; CuA straight and shortened with one row of cells between it and posterior wing margin; area between MP and CuA twice as broad as postdiscoidal area.

***Azarphlebia evanescens* sp. nov.**

(Fig. 1)

Holotype. NIGP173379 (imprint of a complete forewing, broken in its distal third).

Etymology. Named after the vanishing distal part of vein MAa.

Diagnosis. As for the genus. Base and distal third of wing darkened.

Locality and horizon. Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China; Middle–Upper Jurassic, Haifanggou Formation.

Description. Wing 62.5 mm long, 14.6 mm wide, base and distal half of wing relatively darkened; pterostigma

5.0 mm long, 1.0 mm wide, covering five cells; no oblique pterostigmal brace; distance between nodus and pterostigma 16.5 mm, between pterostigma and wing apex 12.5 mm; between wing base and arculus 7.0 mm, between arculus and nodus 23.5 mm, between wing base and Ax1 5.8 mm, between Ax1 and Ax2 5.0 mm; Ax1 and Ax2 of slight inverted obliquity; no secondary antenodals in area between C and ScP, nine secondary antenodals of second row; 18 subantenodal crossveins; discoidal space basally opened; MAb sub-aligned with arculus; two rows of cells in anal area; AA distally fused with CuA; area between MP and CuA twice as broad as postdiscoidal area, with an elongate transverse cell just distal of CuA; CuA shortened, with only one row of cells between it and posterior wing margin; postdiscoidal area with one row of cells; MAa distally zigzagged and vanishing in area between MP and RP3/4; area between RP3/4 and IR2 distally narrowed with one row of cells in-between; base of RP2 aligned with subnodus; area between IR2 and RP2 distally broadened; IR1 well defined, with seven rows of cells and a strong secondary longitudinal vein between it and RP2; five rows of cells between IR1 and RP1; 11–12 postnodal crossveins not well-aligned with 13 postsubnodal crossveins.

Discussion

The general shape of this forewing is typical of the family Isophlebioidea in the rather long and narrow pterostigma in a basal position, very broad area between MP and CuAa, basally widened antenodal area, short CuAa. Even if *Azarphlebia* **gen. nov.** has some characters present in the Isophlebiidae, *viz.*, primary antenodal brackets Ax1 and Ax2 hypertrophied and of distinct and converging obliquity, and basal part of area between MP and CuA twice as wide as basal part of postdiscoidal area; it does not show the other characters of this family, *viz.*, its anal vein AA is reaching CuA; its forewing discoidal cell is opened; the distal side (MAb) of the discoidal cell is not distinctly distal of the arculus; no secondary antenodal crossvein in area between C and ScP (Bechly, 2008).

Azarphlebia **gen. nov.** has the straight and shortened vein CuAa with a very narrow (one row of cells) area between it and posterior wing margin and a long transverse cell appressed to basal part of CuA in area between MP and CuAa, typical of the Middle Jurassic Chinese group of campterophlebiid genera: *Hsiufua* Zhang *et al.*, 2013, *Angustiphlebia* Li *et al.*, 2013, *Parafleckium* Li *et al.*, 2012, *Bellabrunetia* Fleck & Nel, 2002, *Amnifleckia* Zhang *et al.*, 2006, and *Parabrunetia* Zhang *et al.*, 2006.

Unlike all these genera, *Azarphlebia* **gen. nov.** has a particular vein MAa, with its distal part zigzagged and vanishing in the area between MP and RP3/4. Even if some other Campterophlebiidae (*e.g.*, *Sinokaratawia* Nel *et al.*, 2007) also have a distally zigzagged MAa, this vein remains discernable in all other Campterophlebiidae (Nel *et al.*, 1993, 2007: figs 1–3, 2009; Zhang *et al.*, 2006; Li *et al.*, 2012a, 2012b, 2013; Zhang *et al.*, 2013).

Furthermore, *Azarphlebia* **gen. nov.** differs from *Hsiufua*, *Parafleckium*, and *Bellabrunetia* in the broader pterostigma situated in a more distal position (Fleck & Nel, 2002: fig. 1; Li *et al.*, 2012a, 2012b: fig. 1; Zhang *et al.*, 2013: fig. 2). *Azarphlebia* **gen. nov.** differs from *Angustiphlebia* and *Parafleckium* in the basal part of area between MP and CuA only twice as wide as the basal part of postdiscoidal area (Li *et al.*, 2012a, 2013: fig. 1).

Conclusion

The discovery of *Azarphlebia* **gen. nov.** shows that Campterophlebiidae were exceptionally diverse in the Middle–Upper Jurassic Haifanggou Formation at Daohugou, especially those of the group of genera with a narrow cubito-anal area and straight shortened vein CuA. This clade seems to have been restricted to Central Asia and North China. We however need to be prudent with such an assumption because our current knowledge about the whole

fauna of Odonata during this period remains fragmentary, even if it is one of the more complete for the Mesozoic.

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